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Short communication

Productivity of invasive saltmarsh plant *Spartina alterniflora* along the coast of China: A meta-analysis

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ABSTRACT

As an aggressive invasive saltmarsh plant in many places worldwide, *Spartina alterniflora* has a wide distribution range in latitude. Previous studies have explored latitudinal trends in *S. alterniflora* productivity in its native regions using meta-analysis, whereas to the best of our knowledge, that in China as its largest invaded regions have not been reported. In this study, we performed meta-analysis to explore latitudinal trends in productivity as measured by the end-of-season-live (EOSL) biomass of *S. alterniflora* along a broad latitudinal gradient from 24°N to 34°N on the coast of China. The results showed that in stark contrast to the linear decreasing trend found along the East Coast of North America as its native region, the latitudinal variation of the consolidated EOSL biomass along the coast of China exhibited an erratic "W"-shape and fell within the range of variation of the surveyed biomass reported in the literature. Additionally, the EOSL biomass was not correlated with climatic factors, such as the mean annual temperature and mean annual growing degree-days. The results of this study complement the ever-growing literature of *S. alterniflora* in China from a consolidated perspective and indicate that the response of *S. alterniflora* productivity to climate change could be more complicated in invaded regions.

1. Introduction

In recent decades, plant invasions have caused great damage to the structure and functioning of the invaded ecosystems worldwide (Vila et al., 2011). After introduction to the invaded region, invasive plants can disperse beyond the naturalized area and become established across a wide latitudinal range (Blackburn et al., 2011; Liao et al., 2016). *Spartina alterniflora* is a native species in the East Coast of North America, which covers a wide latitudinal range (26°N–46°N) from Gulf Coast to Canada (Kirwan et al., 2009). As an invasive species, *S. alterniflora* rapidly colonizes wide exotic ranges through rapid adaptive evolution in genotypes or phenotypic plasticity (Lee, 2002; Richards et al., 2006). Currently, *S. alterniflora* has spread to estuaries and coastal salt marshes in many places worldwide, including the Pacific Coast of North America, Europe, New Zealand and China, causing serious consequences on the local ecosystems (Feng et al., 2017; Ma et al., 2014; Strong and Ayres, 2016). *S. alterniflora* was introduced to China in 1979 for erosion control, soil amelioration, dike protection, etc. (An et al., 2007). As a result of continuous transplanting and natural dispersal, this species has spread to a wide latitudinal range from Guangxi Province (20°N) to the Tianjin municipality (39°N), making China the world's largest *Spartina*-invaded region (Li et al., 2009; Strong and Ayres, 2013).

Many studies have used field surveys, common garden experiments and meta-analysis to explore the traits of invasive plants, including their morphology, phenology, phenotypic plasticity and genotype, across a wide latitudinal range in invaded regions (Chevin and Lande, 2010; Hodgins and Rieseberg, 2011; Liao et al., 2016; Liu et al., 2016). Some of the studies have explored the relationship between the traits of *S. alterniflora*, such as sexual reproduction, plant height, survival rate, and abiotic factors across latitude along the Coast of China. Specifically, based on the survey results of 26 populations of *S. alterniflora* along the coast of China in July, Zhao et al. (2015b) found that plant biomass and other traits, such as plant height, basal stem diameter as well as population density, were strongly correlated with latitude. Using path analysis method, the authors further identified temperature and precipitation as the key abiotic factors influencing the phenotypic variation of the plant, while pH and salinity played a minor role. Notably, as *S. alterniflora* is at varying stages of the growing season across latitude in July, this sampling strategy has a limitation in reflecting the annual productivity of this species. Liu et al. (2016) studied geographical variation in the vegetative growth and sexual reproduction of *S. alterniflora* across a wide latitude of 19° along the coast of China using both field surveys and common-garden experiments. While strong correlations between plant traits, including plant height, shoot density as well as sexual reproduction, and abiotic conditions, including mean annual

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temperature, growing degree days, tidal range and soil nitrogen content, were identified from the results of field surveys, the same latitudinal trends were not observed in common-garden experiments, suggesting that the latitudinal variation was largely due to phenotypic plasticity. Moreover, plant biomass was not covered in this study.

In addition to field surveys and common-garden experiments, meta-analysis consolidates existing studies from different sources and study sites to minimize the variability from different measurement methodologies used in different studies, as well as the variability that arises from local factors (nutrient, salinity, herbivory, marsh elevation, etc.). Notably, Kirwan et al. (2009) and Turner (1976), among others, have conducted meta-analysis on *S. alterniflora* productivity along the East Coast of North America, where this plant is a native species. Specifically, Kirwan et al. (2009) adopted the end-of-season-live (EOSL) biomass as a proxy for annual productivity of this plant and used data consolidated over a single degree of latitude to minimize the variability mentioned above. The latitudinal trend of *S. alterniflora* productivity was found to be negative, together with positive correlations between biomass and some abiotic factors, such as the mean annual temperature and growing degree-days. To the best of our knowledge, however, the use of meta-analysis to study the latitudinal variation of the productivity of the invasive saltmarsh plant *S. alterniflora* along the coast of China has not been reported in the literature.

In the present study, we used meta-analysis to determine I) the variation of productivity as measured by the EOSL biomass of *S. alterniflora* in different geographical locations along a broad latitudinal gradient on the coast of China, II) how the latitudinal variation of the consolidated EOSL biomass compares with the reported results based on field surveys, and III) how these results compare with reported latitudinal trend along East Coast of North America as the native region. The results of the comparison are explained, and the implications of the results are also discussed.

2. Method

2.1. Database

To compile a comprehensive database, we searched the Web of Science for English literature and the China National Knowledge Internet (CNKI) for Chinese literature. We used the following queries for Web of Science: topical subject (TS) = (*Spartina alterniflora* OR *Spartina-alterniflora* OR *Smooth Cordgrass* OR *Smooth-Cordgrass*) and address = (China), resulting in 682 publications. For CNKI, we used the equivalent terms and expressions in Chinese: TS = (*Spartina alterniflora*) and TS = (biomass), resulting in 291 references, including 198 journal papers and 93 Master's and PhD dissertations.

We examined both Chinese and English references and retained those that (1) were field samplings or control groups in field experiments (not laboratory experiments or remote sensing based studies) on the natural *S. alterniflora* community (not from transplanted or seeded communities); (2) measured and reported EOSL biomass, with a sufficient description of sampling methods and study sites; and (3) did not change plant growing conditions by human interventions, such as mowing, fertilizing, firing and overshadowing, etc. A total of 53 references were retained after screening, of which 23 references were in English and 30 references were in Chinese (including 7 Master's and PhD dissertations). The details are provided in Supplementary material. For each relevant reference, we extracted EOSL biomass data from the text, tables or figures after digitization. We treated the EOSL biomass according to Kirwan et al. (2009). If the references clearly stated that some biomass sampling was conducted at the end of the growing season, then we considered the corresponding value directly as the EOSL biomass. For continuous sampling throughout the growing season, the last reported biomass value was assumed as the EOSL biomass. We also classified the plant ecotype in each study according to the criteria proposed in Ornes et al. (1998), i.e., the tall form is 100–300 cm in height, and the short form is below 100 cm, whenever possible.

2.2. Climatic factors

We collected climatic data including the mean annual temperature and growing degree-days of each study site. The growing degree days of a year can be calculated as the total number of days with mean daily temperatures exceeding 10 °C (a temperature threshold for significant plant growth) in the year, which is a commonly used parameter to represent the length of the growing season (Gray and Mogg, 2001). We obtained the climatic data from the Climate Information for the China Meteorological Data Sharing Service System (http://cdc.nmic.cn/) and selected the station closest to each study site and the years in which the study was performed.

2.3. Statistical analysis

For statistical analyses, we adopted the same method as Kirwan et al. (2009), i.e., assembled EOSL biomass data over a single degree of latitude (± 0.5°) and calculated the average to minimize variability from different measurement methodologies used in different studies, as well as that arising from local factors. We performed regression analysis between EOSL biomass and climatic factors/latitude to explore their potential correlation. All statistical analyses were conducted in SPSS Statistics 20.

3. Results

The 53 references finally retained cover 17 different study sites with a wide latitudinal range from 24°N to 34°N. The distribution of the sites as well as the number of associated studies is shown in Fig. 1. The consolidated EOSL biomass of *S. alterniflora* did not steadily decrease with increasing latitude but rather exhibits an erratic "W"-shape variation trend (Fig. 2). As shown in Fig. 2, the EOSL biomass reaches local maximum at 24°N (2270 $g.m^{-2}yr^{-1}$), 29°N (2040 $g.m^{-2}yr^{-1}$) and 34°N (1821 $g.m^{-2}yr^{-1}$), and it attains a local minimum at 28°N (236.73 $g.m^{-2}yr^{-1}$) and 32°N (1113.15 $g.m^{-2}yr^{-1}$). The error bars in Fig. 2, which represent the variation among the EOSL biomass reported by different studies at the same latitude, indicate significant local and temporal variabilities in EOSL biomass. For example, EOSL biomass at 33°N varies from 466.71 $g.m^{-2}yr^{-1}$ (Zhou et al., 2008) to 3210 $g.m^{-2}yr^{-1}$ (Zhang et al., 2010). Notably, only one appropriate study was found at 28°N, and the reported EOSL biomass is anomalously low for unknown reasons (the open square in Fig. 2). As such, we eliminated it from all subsequent analyses.

Even after excluding the biomass at Leqing Bay, the linearity of the latitudinal trend of EOSL biomass along the coast of China is rather poor ($r^2 = 0.19$, $P < 0.01$). The correlations with climatic factors, such as the mean annual temperature and mean annual growing degree-days, are also weak (Fig. 3). We made further distinctions between different plant ecotypes and found that the identified ecotypes are all tall form, and the selected EOSL biomass of the tall form is not correlated with climatic factors (Fig. 3).

4. Discussion

4.1. Variability of S. alterniflora productivity in China

In this study, we used meta-analysis to explore the latitudinal trends in productivity as measured by EOSL biomass of *S. alterniflora* along a

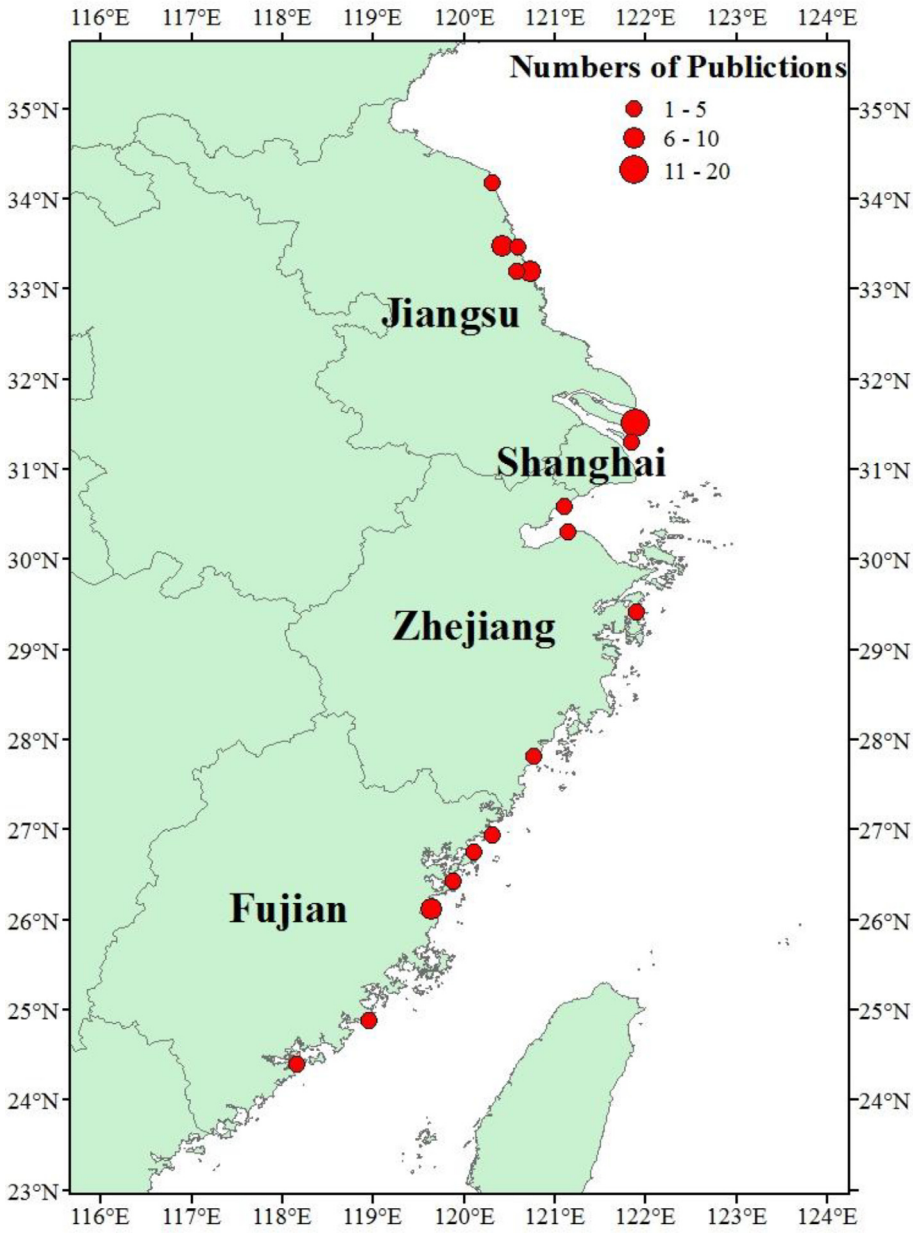

Fig. 1. The distribution of the sampling sites used in the compilation of *Spartina alterniflora* end-of-season-live (EOSL) biomass.

broad latitudinal gradient from 24°N to 34°N on the coast of China. The latitudinal range in this study covers four provincial-level administrative regions, including Fujian, Zhejiang, Shanghai and Jiangsu, which are the main areas of *S. alterniflora* invasion in China (Zuo et al., 2012).

As stated above, the local variability of EOSL biomass throughout China is generally high, which suggests that some local factors, such as salinity, topography, sediment, nutrient, and herbivory, may play important roles in the productivity. For example, the EOSL biomass at Dongtan, Chongming Island (31.53°N) varies from 235.68 $g.m^{-2} yr^{-1}$ (Tang et al., 2012) to 2370.37 $g.m^{-2} yr^{-1}$ (Quan et al., 2007), which may be due to differences in sampling location (e.g., creek bank vs. marsh interior) or invasion history. Moreover, variation in plant ecotype also leads to variability in EOSL biomass. The *S. alterniflora* species initially introduced to China were from three different regions in USA, namely, the tall form from Georgia, the medium form from North Carolina, and the short form from Florida (Qing et al., 2011). Different ecotypes showed significantly different biomass, e.g., biomass for tall and short forms at Sapelo Island, Georgia, were approximately 1000 and 420 $g.m^{-2}$, respectively (Dai and Wiegert, 1996). After being introduced to China, heterogeneous mixtures of both original ecotypes and ecotype hybrids occurred, resulting in a greater variability of *Spartina* biomass in China (Bernik et al., 2016; Xia et al., 2015). Notably, the *S. alterniflora* populations in Jiangsu Province have been recognized as tall ecotype (Zuo et al., 2012); however, the ecotypes of *S. alterniflora* in other areas in China need further confirmation.

The EOSL biomass reaches a prominent local maximum at 29°N (2040 $g.m^{-2} yr^{-1}$), which is located at southern Hangzhou Bay. The salt marshes at Hangzhou Bay were characterized by high nitrogen concentrations due to severe eutrophication at the bay (Wang et al., 2011). As nitrogen is considered a primary resource limitation on the growth of *S. alterniflora* (Darby and Turner, 2008; Qing et al., 2012), the

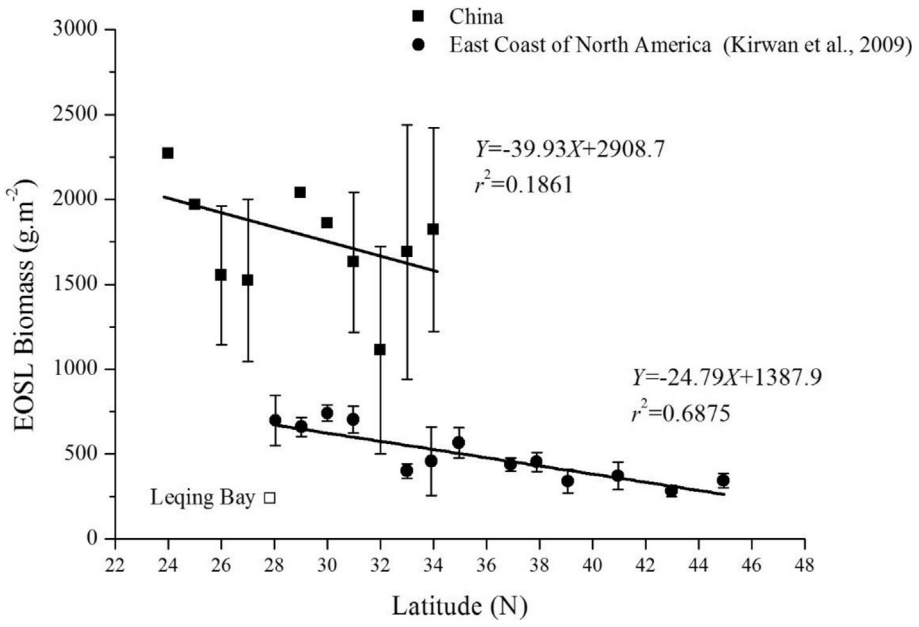

Fig. 2. Consolidated end-of-season-live (EOSL) biomass of *Spartina alterniflora* across latitude along the coast of China versus that along the East Coast of North America.

severe eutrophication may result in a locally increased EOSL biomass. Similarly, a suitable ecological niche, e.g., fine sediment particles and weak currents (Zuo et al., 2012), as well as relatively lesser interspecific competition (Chung, 2006) at sites in Jiangsu Province (33-34°N), also rendered their EOSL biomass higher than those at sites lower in latitude.

4.2. Comparison of latitudinal trends of productivity

Based on the survey results of 26 populations of *S. alterniflora* along the coast of China, Zhao et al. (2015b) reported that the overall trend of variation showed a two-hump shape (Fig. 4), i.e., similar strong nonlinearity. Although the biomass was surveyed in July in Zhao et al. (2015b), Fig. 4 shows that the consolidated EOSL biomass primarily falls within the range of variation of the surveyed biomass. Notably, according to Zhao et al. (2015b), the sampling site with a much larger biomass at approximately 38°N was located near Tianjin, where *S. alterniflora* was mainly distributed along the river mouth and presumably strongly influenced by eutrophication.

Fig. 2 shows the comparison of the present meta-analysis results with that reported by Kirwan et al. (2009). Clearly, the *S. alterniflora* productivity and its latitudinal trend of variation along the coast of China is vastly different from that in its native region. The fitted trend line in China shows a much steeper slope and larger intercept than that in the native region, indicating that the *S. alterniflora* biomass is larger and has a stronger dependence on latitude in China. If we extrapolate the trend line in the native region to 24°N, then the resultant EOSL biomass will be 792.94 $g.m^{-2}$, which is approximately one-third of the EOSL biomass at 24°N in China.

Field observations and common garden experiments have previously shown that rapid evolutionary changes of *S. alterniflora* in some performance-related traits, including their morphology, biomass allocation and phenotypic plasticity, occurred after their introduction to China (Qing et al., 2012; Qing et al., 2011; Shang et al., 2015). Phenological points of both the tillering and flowering of invasive *S. alterniflora* populations were ahead of native populations in common garden experiments, suggesting that *S. alterniflora* enjoys a longer growing season for a larger biomass and greater competitive advantage in sexual productivity in invaded regions (Shang et al., 2015). Moreover, a higher photosynthetic rate of *S. alterniflora* relative to competing native plants was also observed (Qing et al., 2012).

In addition to self-adaptive evolution mechanisms, external factors, such as herbivory and eutrophication, also play important roles in improving plant growth. While *S. alterniflora* is subject to an herbivory effect from *Littoraria irrorata* and *Melanoplus* spp. in its native region, the attacks by herbivores and pathogens are reduced in invaded regions, enabling the plant to allocate less resources to herbivore resistance and increase allocation to its growth and reproduction (Blossey and Notzold, 1995; Johnson and Jessen, 2008; Silliman and Bortolus, 2003; Silliman et al., 2004; Silliman and Zieman, 2001). As previously described, as a N-limited plant, the growth of *S. alterniflora* is highly dependent on the exposed level of nitrogen (Darby and Turner, 2008; Tyler et al., 2003). Higher nitrogen contents also help invasive *S. alterniflora* to strengthen its leaf structural defenses and prevent this plant from herbivory (Qing et al., 2012). In general, coastal eutrophication in China is much more severe than that in the East Coast of North America, and this gap has been increased over the past two decades, greatly contributing to the increased biomass and promoting the invasion of *S. alterniflora* (Zhao et al., 2015a).

4.3. Implications for the response of S. alterniflora productivity to climate change

Based on the compilation of 56 biomass samplings, Kirwan et al. (2009) conducted a meta-analysis showing that the annual productivity exhibited a positive linear correlation with the mean annual temperature. Further assuming that local variables remained constant, Kirwan et al. (2009) predicted that an increase in mean annual temperature of 2–4 °C by 2100, a widely adopted IPCC scenario, would increase productivity by approximately 50–100 $g\,m^{-2}\,yr^{-1}$. However, given the weak correlations between EOSL biomass and latitude/mean annual temperature shown in this study, presumably due to the effects of local disturbance, the quantitative extrapolation to future climate change scenarios seems unreasonable and is therefore not attempted herein.

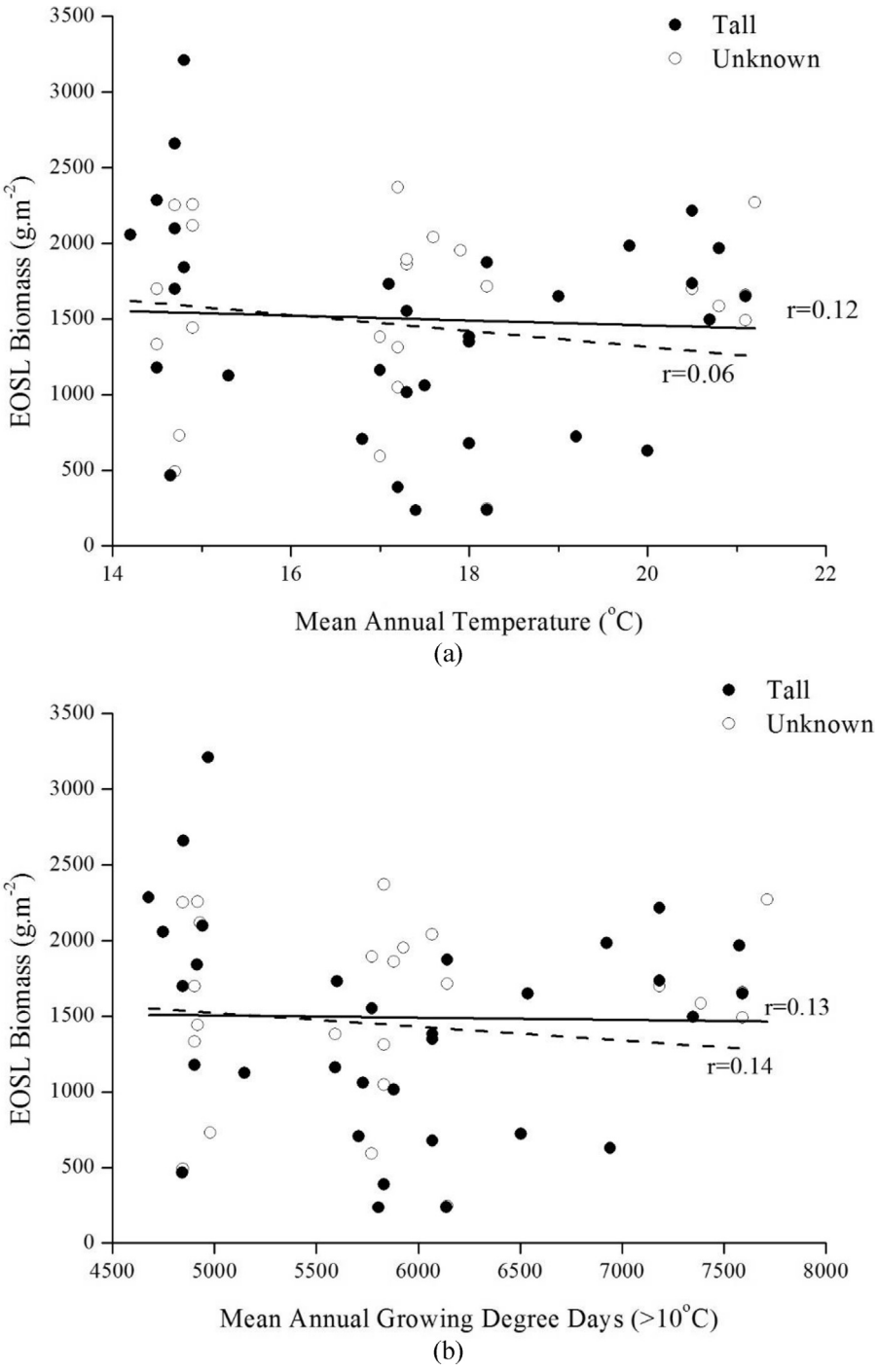

Fig. 3. Correlations between end-of-season-live (EOSL) biomass and climatic factors: (a) mean annual temperature, (b) mean annual growing degree days (> 10 °C), dashed line represents linear curve fitting for the tall form, and solid line represents linear curve fitting for all data.

Nevertheless, previous experiments conducted for *S. alterniflora* in both invaded and native regions reported that the optimal temperature for light-saturated net photosynthesis and net carbon assimilation is consistently 30–35 °C (Ge et al., 2014; Giurgevich and Dunn, 1979). Hence, we speculated that the annual productivity of *S. alterniflora* may increase in warmer temperatures in Shanghai and Jiangsu Province, where the current temperature throughout most of the growing season still falls below the optimal temperature. Whereas for areas further south, e.g., Fujian Province, where the current temperate throughout the growing season is closer to the optimal temperature, a reduced cold period caused by global warming may affect vernalization, which could reduce the germination rate and adversely affect *S. alterniflora* productivity (Guo et al., 2013). Moreover, at lower-latitude regions from Guangxi to Fujiang Province, there is a significant niche overlap between *S. alterniflora* and mangrove (Chen et al., 2009), and exotic mangrove species have been widely transplanted in southern China to promote mangrove restoration and control *S. alterniflora* invasion (Zhou et al., 2015), which poses another limiting factor for *S. alterniflora*.

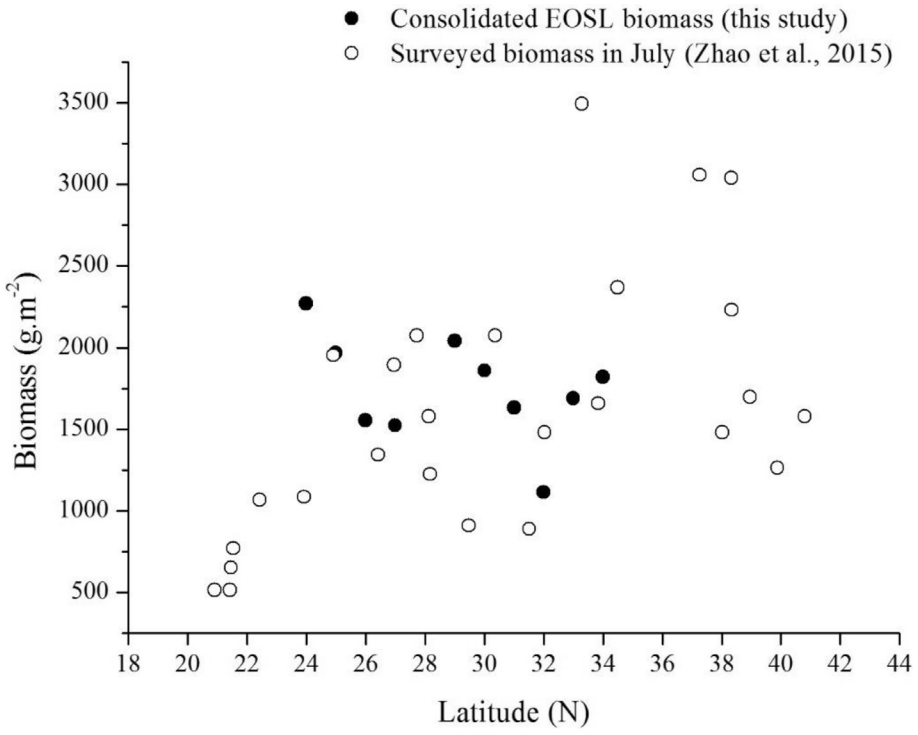

Fig. 4. Consolidated end-of-season-live (EOSL) biomass versus surveyed biomass of *Spartina alterniflora* across latitude on the coast of China.

5. Conclusion

The meta-analysis performed in this study provides an overview of the productivity of *S. alterniflora* across latitude along the coast of China. The results showed that in stark contrast to the linear decreasing trend found along the East Coast of North America as its native region, the latitudinal variation of consolidated EOSL biomass along the coast of China exhibited an erratic "W"-shape and yet fell within the range of variation of the surveyed biomass reported in the literature. The EOSL biomass also did not correlate with climatic factors, such as the mean annual temperature and mean annual growing degree-days. This contrast is presumably due to the rapid evolutionary changes in performance-related traits, lack of herbivores, eutrophication, etc. If temperature continues to warm in the coming decades, then we speculate that the productivity of *S. alterniflora* may increase in mid- and high-latitude regions of China and decrease in low-latitude regions. Furthermore, the meta-analysis results presented are subject to major assumptions and uncertainties, e.g., EOSL biomass and latitudinal average, and hence should be viewed as a supplement rather than substitute to standardized sampling in studying latitudinal trends.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecoleng.2018.03.015.

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